

Robbie Burns revisited

Whatever the precise conception of the content of episodic-like memory, these studies suggest that at least some animals can mentally travel back to their past. However, the concept of mental time travel we introduced at the beginning goes beyond episodic memory, as Robbie Burns alluded to in his original lament. For, when filled with remorse over the fate of the field mouse he concluded that being stuck in the present was a blessing:

*But oh I cast my eye on
prospects drear,
and forwards tho' I canna see,
I guess and fear.*

This forward-looking aspect of mental time travel is only just beginning to be explored in animals. It may also provide the key to understanding episodic memory's errors: for a memory that reconstructs pieces of the past can also reassemble them into imaginary future scenarios. As Mark Twain noted so judiciously: "My life has been filled with many tragedies, most of which never occurred."

Where can I find out more?

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Essay

All the queen's men

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Humans have an ancient and intimate relationship with honey bees — from the development of beekeeping in prehistoric times up to the recent sequencing of the honey bee genome. Yet, the intimacies of bee sexuality remained obscure and contentious until relatively recently. Their stepwise unravelling is a tale of advances and misconception that, in part, may have stemmed from an all too humanised view of bees.

Humans and bees have had a long lasting relationship that consisted mainly of humans robbing the bees of their honey. This relationship dates back to ancient hunter-gatherer cultures and probably to non-human ancestors. Even in prehistoric times, humans had quite sophisticated techniques for dealing with bees; cave paintings show how ladders and ropes were used to get at the bees (Figure 1) and how smoke was used to calm them. Certainly, by the 3rd millennium BC in ancient Egypt, beekeeping had developed into a fully fledged sophisticated practice, with specialised beekeeping techniques and man-made hives, which have largely remained unchanged over the centuries.

The Egyptians worshipped bees and thought that they stemmed from tears shed by the sun god Ra. As a hieroglyph the bee symbolised lower Egypt (Figure 1).

Successful beekeeping and honey harvesting obviously required a detailed knowledge about bee biology, of their sensory capabilities, their life cycle and how they propagate. But just how detailed did that knowledge have to be? And what aspects did it entail? It turns out that, despite having achieved great sophistication in bee management, humans were, until relatively recently, surprisingly ignorant about essential features of bee biology, in particular bee sex. This may be because, until recently, bees

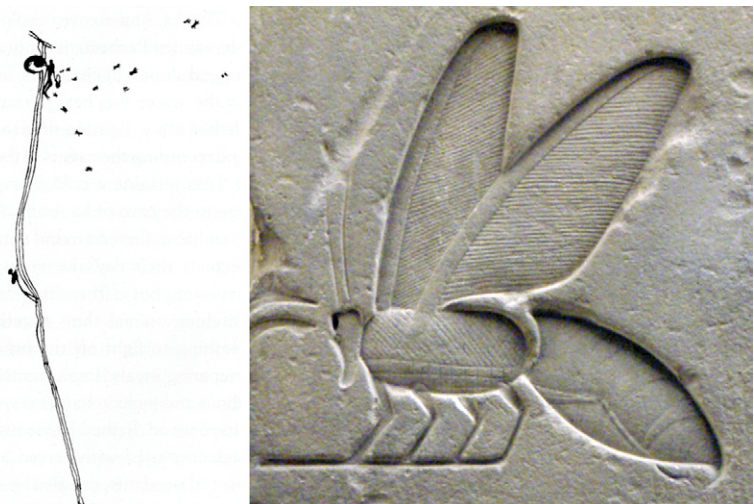


Figure 1. An ancient love affair.

A cave painting (left) from La Araña Cave in Spain showing Neolithic honey collection using ladders or ropes (With permission from *Letters from the Hive* p12, Bantam Books). A hieroglyph of a bee (right), symbolising Lower Egypt from the tomb of pharaoh Senusret I, from his 'sedge and bee' title. (From <http://commons.wikimedia.org/wiki/Image:AncientEgyptianRelief-BeeHieroglyph-ROM.png>)

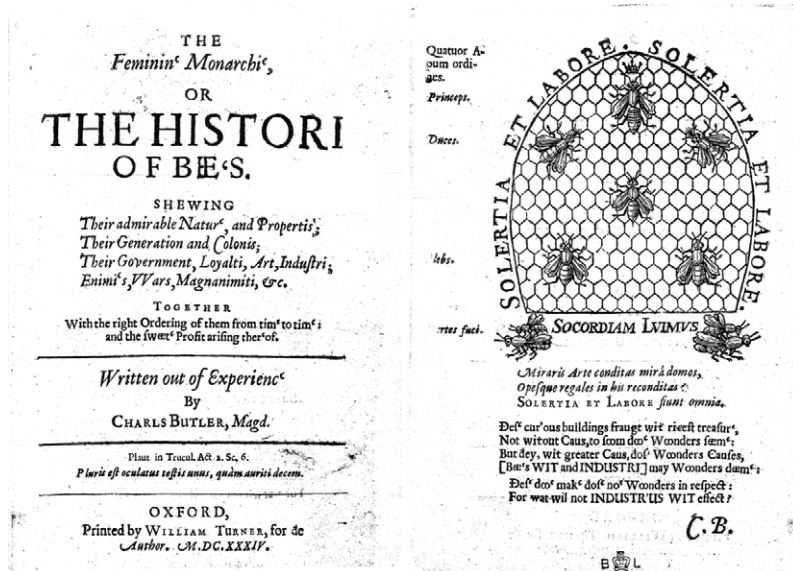


Figure 2. The feminine monarchy. Frontispiece (left) and first page (right) of third edition of Charles Butler's *Feminine Monarchie*, published in 1634. The first page depicts the four orders according to Butler. From the top: Queen, 'duces' people (plebs) surrounded by the motto: *Solertia et labor* (sagacity and work). Drones being removed by workers are shown at the bottom with the inscription *socordiam luimus*, 'for idleness we atone'. (With permission from the British Library.)

were not properly domesticated, in the sense that they were not bred selectively – instead, reproduction was left up to the bees. Thus, knowing about honey bee sex was of no immediate interest to beekeepers and only became a matter of interest when scientists turned their attention to bees.

The battle over the sexes

As with most areas of science, the first written account of bee sexuality can be found in the writings of Aristotle. In his *History of Animals* the philosopher gives an account of what was known about bees two and a half thousand years ago. Aristotle recognised up to nine different sorts of 'bees' – not all of which actually are bees – among them two kinds of 'kings' (βασιλευς) and the drone, which "is the largest of them all, has no sting and is stupid". He grouped together the working bees and the 'kings', but regarded the drones as members of a separate species that "only injure the other bees" – a notion for which he took the so-called 'drone battle' as evidence.

The recognition of a special, ruling bee is surely an ancient feature and the role it is attributed may reflect peculiarities of the local social system; in Oman for instance, the casts of the bee *Apis florea* are referred to as 'sheikh', 'people' and 'slaves', which refers to the dark coloured drones of this species. The likening of the hive-life to human society is a recurring theme and – along with the proverbial assiduity of the 'working' bee – the organisation of the bee-state has especially in pre-modern times been used as a model for how humans should live together. It is conceivable that these analogies have also contributed to obscuring how different bees are.

Apart from seemingly absurd concepts such as bees storing noises in earthen vessels and carrying stones with them to avoid getting carried away by the wind, Aristotle had an impressive grip of the goings on in the hive. He described the various cells for bees, rulers and drones, the way the grubs were fed and cared for and the division of labour in the hive. He

had observed bees swarming and following their 'king'. But he was uncertain about how bees reproduce, or in fact if they reproduce at all. Aristotle quotes several prominent concepts of the day, such as bees finding and collecting their offspring in flowers of various plant species, in particular olives – it had been noted that in years rich in olives there were also many bees. Quite literally, bees were presumed to grow on trees.

Aristotle's ideas shaped the way people thought about bee biology for almost two millennia and were propagated by the writings of other antique eminences such as Pliny or Virgil. While practical beekeeping progressed, the uncertainty about how bees did it remained high. Concepts that are close to what we know today – the Anglo-Saxons for instance called the Queen 'beo-mother' or '*mater apiorum*' – coexisted level with ideas of spontaneous generation, such as bees emerging from 'corruption'. As late as the 17th century, beekeeping books even contained recipes as to how to make bees. One source suggested to kill an ox and leave it in a locked chamber for 45 days and granted that "there will proceed from it an infinity of bees". Many apiarists' careers – and many oxen's lives – may have been ruined that way.

In the 17th century, things changed with the publication of two landmark books – Charles (sic) Butler's *Feminine Monarchie* (Figure 2) and Samuel Purchas' *Theatre of Politicall Flying Insects*, the latter of which came out forty years later and largely reiterated Butler's points. Both books were centered not so much on the practice of beekeeping but on their natural history and shaped a view of bee biology that went beyond Aristotle. Charles Butler (1560–1647) was a vicar in Hampshire and – aside from his bee fancy – was an active proponent of a reform of English spelling, as reflected in the way he spelled his first name. In 1609, he published his

Feminine Monarchie, which was widely read and popularised the view that the ruler of the hive was indeed a queen. Perhaps not surprising, the book was published just 6 years after the death of Elizabeth I, such that the notion of a female rules may not have been that strange to him. Butler gives no reason for what led him to take on this notion. In fact, that the queen is a female had been noted twenty years before by a Spanish apiarist, Luis Mendez de Torres, but Butler did not seem to have known of his work; after all, the frontispiece of his book states that Butler derived his knowledge “out of experience” (Figure 2).

Butler puts forward arguments to show that the drones are the males and not “made of a honey bee that has lost her sting; which is as likely as that a dwarf having his guts pulled out should become a giant”. As he had observed droneless hives becoming infertile, he concluded that they were required for reproduction, a fact that had escaped Mendez. The fact that there is a considerable time of the year when there are no drones disproved Aristotle’s notion of drones breeding drones. But apparently, the notion of the queen giving birth was alien to Butler, who grew up under the reign of a virgin queen. Thus he concluded that the workers generated the offspring by mating with the drones. He also had ideas about how the nobility arose: “the lady bees are bred in several palaces of the queen after a peculiar and more excellent manner. For the golden matter whereof they are made, is not turned into a worm, but immediately receives the shape of a bee”; this latter idea goes back to Aristotle.

In addition to these three castes, Butler believes to have observed a fourth caste, which he referred to as governors and leaders, some of which “stand upright” and guard the queen. Again, his analogy of the beehive as a “perfect monarchy, the most naturall and absolute form of government” may have misled him. Pure reasoning and

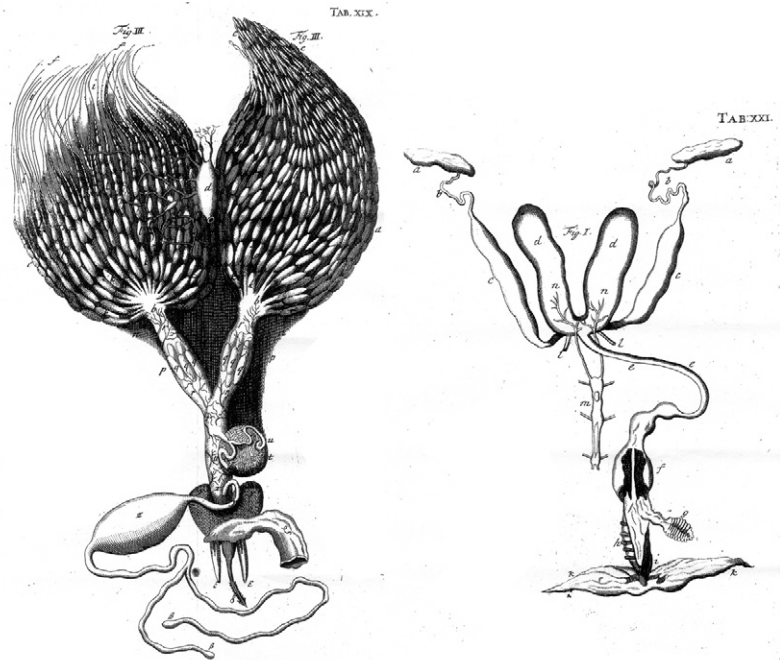


Figure 3. Beautiful evidence.

Illustrations from Jan Swammerdam’s *Bybel der Natuure*, showing the reproductive duct of a honey bee queen (left) and a drone (right). (With permission from the British Library.)

analogies were clearly of limited use for the understanding of bee biology, and real hard evidence, data, were needed. It took a scientist to provide them.

Jan Swammerdam (1637–1680) was an eminent pioneer of anatomy and in his life of less than fifty years he made several seminal discoveries, such as the eggs in the human ovary. His observations on insect anatomy and development were pivotal in doing away with previous notions of spontaneous generation and formulating one of the fundamentals of biology, namely that “all animals hatch from eggs that are laid by a female of the same species”. Swammerdam had been trained within a school of great Dutch anatomists, but soon turned his attention away from the human body. With the use of sophisticated dissecting equipment and microscopes he was the first to peer inside many insects, among them honey bees.

His findings are summarised in a set of beautiful illustrations (Figure 3) in his *Bybel der Natuure*, which appeared in print

only in 1737 and whose title aptly reflects its copiousness, the scale of the task and not least the religious obsession of the author. Swammerdam saw that the queen contained fully developed ovaries with eggs and a sperm receptacle and thus concluded “that the king, as commonly called, was a female”. Notably, Swammerdam never uses the term ‘queen’. This may have to do with his republican disposition as a Dutchman, or with his Christian attitude towards insect societies: “there is no superiority or pre-eminence among either Bees or Ants; love and unanimity, more powerful than punishment or death itself, preside there, and all live together in the same manner as the primitive Christians anciently did, who were connected by fraternal love, and had all things in common.”

Swammerdam proved that the drones are males based on the similarity of their genitals to those of males of other species. He also commented on the sex of the workers: “the common working bees approach nearer



Figure 4. The blind beekeeper.

François Huber's work was pivotal in elucidating how bees reproduce (from Huber's *New Observations on Bees*, British Library).

to the nature and disposition of the females than the males" and "have no ovary, and therefore, like women who have lived virgins till they are past child bearing, serve only the purpose of labour". From his anatomical observations, he could conclude about how bees reproduced, namely that "the female lives in the hive for no other purpose but to deposit, as occasion offers, her eggs" and that "it is the business of the males to impregnate these eggs". Yet, as powerful his anatomy based reasoning was, it also misled him. From the anatomy of the drones' genitalia, he concluded that there was no conceivable way they could be used to mate with the female, they simply wouldn't fit. He seemed to have believed in his anatomical reasoning more than anything and concluded that bee sex must involve something else than copulation. This led him to invoke the idea that "the female among the Bees is impregnated in a peculiar manner, merely by odoriferous effluvia", which he termed '*aura seminalis*'. While Swammerdam even proposed an experiment to test this concept he never did it and another century was to pass till he was eventually disproved.

The riddle of reproduction

As Swammerdam's misconception about mating

illustrates, anatomy had its limitations as a source of clues about bee behaviour, in particular the pressing question of if and how female bees are fertilised. Answering this question was facilitated by the seemingly simple invention of hives with glass windows. Among the first to systematically use such hives was the French polymath and inventor René-Antoine Ferchault de Réaumur (1683–1757), who initiated direct, manipulative experimentation on bees. Réaumur observed how eggs were laid and how the brood developed in unprecedented detail. Réaumur also discovered the temperature regulation of the hive – he had as it were a natural interest in temperature, as he had invented the ethanol based thermometer and a temperature scale bearing his name. Réaumur used paint to mark bees and investigated the fate of queenless colonies as well as that of introduced queens. In his *Memoires pour Servir a l'Histoire des Insects* of 1740 he described in great detail the anatomy and life of the honey bees. Despite his meticulous observations of life inside the hive, based on which he proved that all offspring is derived from the queen, Réaumur had never actually seen a queen mate. He tried to lock up virgin queens with drones in glass boxes to force them to mate, but had no success.

It was left to François Huber (1750–1831), a Swiss naturalist and probably the first specialised bee researcher, to solve this mystery. Huber (Figure 4) was blind from a young age and relied on his skilled assistant François Burnens to execute and document the experiments he had designed and interpreted. Huber and Burnens used systematic experimentation to disprove earlier ideas about fertilisation of the queen, in particular Swammerdam's *aura seminalis*. They placed a pierced container with drones into a sealed hive from which all males had been removed and which only contained virgin queens. As no offspring emerged, Huber

concluded that more than just the drones' odour was required to do the job – an experiment that, as he somewhat smugly notes, Réaumur had failed to do.

Another widespread idea at the time was that the queen in her nobility did actually not require the common act of fertilisation, but could instead self-fertilise – a notion which was supported by previous observations that droneless hives can generate offspring. When Huber and Burnens sealed a maleless hive and placed virgin queens within, again no offspring emerged. The same result was obtained when males were locked in the hive with the virgins, from which he concluded that fertilisation must take place outside the hive.

Eventually, in June 1788, Huber and Burnens observed a queen leaving a hive, followed by drones, and returning not before long covered with fertilisation marks and filled with male seminal fluid. While Huber's research, published in 1806 settled the debate over reproduction and popularised the idea of the mating flight, he was in fact not the first to have observed it. Fifteen years before Huber, a scientific maverick, the Slovenian beekeeper Anton Janscha, had actually published an account of a mating flight which went largely unnoticed.

Dealing with determination

François Huber also provided evidence that aided the breakthrough of understanding how the difference is determined between queens and workers, which were known to both be female. In 1760, a German priest, Adam Gottlob Schirach (1724–1773), had observed what happens to a beehive lacking a queen. He noted that, as soon as the queen is missing, the workers begin to enlarge some of the cells containing worker brood and feed the grubs more and a different diet. If worker grubs were placed in these cells, they became queens. The obvious conclusion was that the queens were not naturally different or special, but that

nurture determined which grubs became queens. This notion was greeted with great scepticism and outright hostility, perhaps not the least because it went against the *zeitgeist* of a natural hierarchy that applied to rulers, no matter if they ruled bees or humans. Through systematic experimentation, Huber confirmed and popularised this concept in a world that by then was perhaps more ready to accept it, having seen kings beheaded and others rise in their place.

Another clergyman, the Silesian Jan Dzierzon (1811–1906), provided a possible explanation for how the other major type of bee, the drone, was determined. Dzierzon was the most eminent apiarist off his time — he corresponded with Mendel and the only bee researcher in whose honour a whole town was named (Dzierzoniów). He did a great deal for improving bee-keeping techniques; he also was a meticulous observer and experimenter. He found a way of distinguishing optically between fertilised and unfertilised eggs, both of which were contained in a mated queen.

Based on the fact that a queen that can leave the hive but not fly to mate only produces drones, he suggested that the drones arise from unfertilised eggs while workers (and queens) come from fertilised ones. He reasoned that, while “in higher animals the male is the perfect and ruling creature [...], the reverse of this takes place in Insects. In the [...] bees, the perfect female forms the central point and holds the swarm together”. Thus, drones, being simpler, were easier to make, without male input. He published his, at the time, politically highly incorrect view in a beekeeper’s newsletter in 1835 and again was faced with considerable scepticism — no surprise as at that time, almost 200 years after Swammerdam, beekeepers in such journals were still debating whether drones really were males.

Once again, it took a member of the scientific establishment

Box 1

Shakespeare on bees.

*So work the honey-bees;
Creatures that, by a rule in nature, teach
The art of order to a peopled kingdom.
They have a king, and officers of sorts,
Where some, like magistrates, correct at home;
Others, like merchants, venture trade abroad;
Others, like soldiers, armed in their stings,
Make boot upon the summer’s velvet buds,
Which pillage they with merry march bring home
To the tent royal of their emperor;
Who, busied in his majesty, surveys
The singing masons building roofs of gold;
The civil citizens kneading up the honey;
The poor mechanic porters crowding in
Their heavy burdens at this narrow gate;
The sad-eyed justice with his surly hum,
Delivering o’er to executors pale
The lazy yawning drone!*

William Shakespeare, King Henry the Fifth, Act I, Scene 2.

This part of a speech delivered by the Archbishop of Canterbury nicely illustrates how humans saw bees. Despite being more bleak and free of the moralistic bias with which other authors saw the bee hive as the model of an ideal society, Shakespeare uses the same analogies that have shaped thinking about bees for centuries.

to settle the controversy in the favour of the unexpected claim. In 1857, Theodor von Siebold, a professor of zoology in Munich with a keen interest in parthenogenesis, defended Dzierzon’s hypothesis. He based this on breeding experiments done by August von Berlepsch in the 1850s, around the same time that Mendel began breeding his peas. These experiments had revealed that when bees of the lighter, ‘Italian’ subspecies of bee were mated with the darker, ‘German variant’, the appearance of the drones always followed that of the queen, while worker offspring was mixed and variegated. In addition, Siebold, subjected eggs from drone and worker cells to close microscopic scrutiny and saw the sperm, the “seminal filament”, only in the worker eggs but never in the eggs that were in drone cells. Thus, male bees must develop from unfertilised eggs.

This idea of haplo-diploid sex determination that is widespread in hymenopterans was later confirmed cytologically by looking at chromosome numbers in male and female bees and culminated in the cloning of the honey bee sex determining locus *csd* in 2004.

In retrospect, it seems puzzling that these basic aspects of bee sexuality took so long to figure out. It perhaps reflects the fact that for successful beekeeping this knowledge was not required and that it took dedicated scientific investigation to solve it. The idealisation of the ‘bee state’ and its perceived similarity to human society may have led to perceiving similarities were there indeed were vast differences (Box 1). However, at least the realisation of a society dominated by females may have been ahead of its time.

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